Termites (Isoptera) in Western Australia: present and future directions of ecological research

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Abstract

The present study reviews the extent to which termite abundance and species richness (alpha diversity) has been measured for major vegetation and disturbance types in Western Australia, critically examines sampling methodologies and suggests priorities for future research.

Termite abundance and species richness (at the site level) are best documented for eucalypt woodlands and heath/shrublands, and are least well documented for eucalypt forests, *Banksia* woodland, mallee, mulga woodland/shrubland and hummock grasslands. Of the disturbance effects, most is known about habitat fragmentation, livestock-grazing, regenerated farmland and rehabilitated bauxite mines; least is known about the effects of fire, and termites in cultivated soils or under exotic timber plantations.

Sampling methods vary widely but fall into two major groups. Firstly, termite-only studies used soil-trenching/skimming and hand-collecting from mounds, surface wood, stumps, roots, *etc.* Secondly, broad-based investigations, covering a range of arthropod taxa, used various combinations of soil and litter cores/quadrats and pitfall traps. Most broad-based studies were carried out in eucalypt forests of the south-west, with an emphasis on the effects of fire. No fire study has measured termite species richness, and most broad-based (and all fire) studies were restricted to three or less study sites, with no replication for treatments (*e.g.* burnt-unburnt). Lack of replication makes it difficult to identify treatment effects from natural variation.

Termite species richness has been found to be a valid surrogate for termite abundance (dry biomass) for south-west ecosystems (eucalypt woodland, mallee, shrubland; Abensperg-Traun & De Boer 1990).Termite genus richness has been found to be the most effective surrogate for species richness in rehabilitated minesites (Nichols & Bunn 1980) and jarrah forest (Bunn 1983), but declined in efficiency for more species-rich ecosystems where a small number of genera contribute most species. Mean species-to-genus ratios were 1.08 for jarrah forest and rehabilitated minesites, 1.49 for gimlet (*Eucalyptus salubris*) woodland (Abensperg-Traun *et al.* 1996b), 1.52 for wandoo (*E. capillosa*) woodland (Abensperg-Traun 1992) and 1.66 for shrubland (Abensperg-Traun unpublished).

Sound ecosystem management requires adequate knowledge of spatial patterns of the abundance and diversity of the biota, as well as their role in ecosystem processes. Current ecological knowledge of the Western Australian termite fauna is inadequate in the following areas;

- the effects of fire on termite abundance and species richness in eucalypt forests and hummock grasslands;
- termite abundance and species richness in spatially extensive but poorly-sampled vegetation types - mallee, mulga woodland/shrubland and hummock grasslands;
- the effects of harvester termites on ecosystem properties in arid and semi-arid (pastoral) regions, particularly in the presence of livestock during drought conditions;
- the relationship between the effects of disturbance on termite communities, and ecosystem function; and
- interactions between termites and other components of the invertebrate fauna, particularly with ants as termite predators.

Introduction

Termites are social insects of predominantly tropical and subtropical regions which account for about 75 % of the land surface of Australia, and more than 80 % of Western Australia. Across the continent, these environments support large termite populations and have a high species richness (Matthews 1976; Braithwaite *et al.* 1988; Stafford Smith & Morton 1990; Whitford *et al.* 1992). There are 260 described Australian species, of which 153 species occur in Western Australia (extracted from data given in Watson & Abbey 1993). The species richness of termites in the mediterranean south-west of Western Australia, for example, is unusually high, relative to its latitudinal position, and rivals the richness of tropical termite communities (Abensperg-Traun & Steven 1997).

There are probably few Western Australian environments where termites are not abundant and diverse, indicating their high functional importance such as their contribution to nutrient-cycling processes (Park *et al.* 1994; Lobry de Bruyn & Conacher 1995) and as food for insectivores (Abensperg-Traun 1994). Areas which support low numbers and few species include some of the southern-most areas (south-coastal; Abensperg-Traun & Milewski 1995). Unpublished personal observations also indicate that areas of high soil salinity (*e.g.* natural salt lake basins and secondarily saline areas with high water tables), and those subject to seasonal flooding, support few termites.

The retention of native habitat as functioning ecosystems, with its component biota, is at the core of nature conservation. Effective ecosystem management necessitates a sound understanding of spatial patterns of faunal abundance and diversity (species richness), and the extent to which different kinds of disturbance factors (*e.g.* fire, habitat fragmentation, livestock-grazing) impact on these community parameters.

Most of Western Australia is subjected to one or more types of habitat disturbance at different spatial scales and levels of intensity, and this impacts on various components of the soil and litter fauna, including termites (Abensperg-Traun & Steven 1996; Majer & Beeston 1996). One current controversy, for example, is how the regular use of fire as a management tool for fuel reduction in south-west eucalypt forests/woodlands may affect the native biota (Christensen & Abbott 1989; Abbott & Christensen 1994; Friend 1995; Calver *et al.* 1996). An added complication to resolving disturbance effects is that the abundance as opposed to species richness of subterranean termite populations is notoriously difficult to quantify because of their highly aggregated distribution in the soil matrix (*e.g.* Nutting & Jones 1990; Eggleton & Bignell 1995). This has obvious implications for studies of disturbance effects where termite communities in undisturbed and disturbed environments are compared.

The present study synthesizes current knowledge of Western Australian termite communities. It reviews the extent to which termite abundance and species richness has been measured for major vegetation and disturbance types, and critically examines the sampling methods used. It then suggests priorities for future research.

Methods

All published ecological studies of Western Australian terrestrial arthropod communities were reviewed for termite coverage. Studies that measured termite abundance and/or species richness were examined for the sampling methods and the broad vegetation and disturbance types that were investigated. The major vegetation types considered were *Eucalyptus* forest, *Eucalyptus* woodland, *Banksia* woodland, mallee (*Eucalyptus* spp), mulga (*Acacia aneura*) woodland/shrubland, heath/shrubland and hummock (spinifex) grassland (*Triodia* spp, *Plectrachne* spp). Types of disturbance that I considered were fire, livestock-grazing/trampling, regenerated farmland, rehabilitated minesites, pine plantations, dieback fungus (*Phytophthora cinnamomi*), habitat fragmentation (remnant size and spatial isolation), and termite communities under pasture/wheat-lupin stubble. As a measure of sampling

effort for vegetation and disturbance types (across discrete studies), I calculated total numbers of study sites at which termite abundance and/or species richness was assessed. I also examined dimensions of sample units (*e.g.* core width/depth) and numbers of samples collected from study sites. Further, I compared sampling methods used by studies that examined termites only, compared with studies where termites were only one component of a range of soil and litter arthropods investigated, because broad-based studies are likely to use a limited range of methods to cover as wide a range of arthropod groups as possible, resulting in sampling inefficiencies for some taxa. The sampling methods used included soil-trenching/skimming (for details on soil trenching, see Abensperg-Traun & De Boer 1990). This involves intercepting termite foraging galleries and chambers in the top 5 to 10 cm of the soil using a spade and extracting the termites *in situ* by hand. Other sampling methods were soil cores, litter cores (where soil cores incorporated the litter component), litter quadrats, pitfall traps, wooden baits and general hand-sampling where termites were sampled from mounds, dead and decomposed surface wood, roots and stumps, and the leaf litter.

Results

Sampling methods

Studies of termite communities in eucalypt forests used the widest range of sampling methods but never used soil-trenching/skimming; only one study was based on general hand-collections (Bunn 1983). Soil cores, soil and litter cores, and litter quadrats were used most often in eucalypt forests (Table 1). Two studies also used litter quadrats in addition to soil cores, and two studies used pitfall traps only. Soil-trenching/skimming coupled with hand-collections were used most often for eucalypt woodlands and heath/shrublands (Table 1). Only one study (with one study site) used a baiting technique. Most studies used more than one method, and they formed two broad groups; one used soil-trenching/skimming and general hand-sampling, while the second used various combinations of soil and litter cores, litter quadrats and pitfall traps.

With regard to disturbance effects, the widest range of sampling methods was used for the fire studies (Table 1). All work on rehabilitated mine-sites used general hand-sampling only, and the single study of dieback used soil cores and litter quadrats. All other studies used soil-trenching/skimming and general hand-sampling; one study of termites under cultivation used soil cores (Table 1).

In terms of numbers of discrete studies, the effects of fire have been examined more often than any other disturbance factor. When fire studies were further examined for sampling methods and vegetation types, studies in eucalypt woodland, mallee and heath/shrubland vegetation were based almost entirely on data from soil-trenching/skimming and general hand-collecting (Table 2). Fire studies in eucalypt forests, in contrast, were based entirely on data from soil/litter cores, litter quadrats and pitfall-traps (Table 2).

The general pattern for disturbance studies was as for vegetation types; studies that used soil-trenching/skimming and hand-sampling, versus studies that used cores/

Table 1

Numbers of study sites for different sampling methods that were used for the assessment of termite abundance and/or species richness for vegetation and disturbance types. Source of data: Davies (1970); Perry (1972); Abbott *et al.* (1979); Abbott & Parker (1980); Nichols & Bunn (1980); Whelan *et al.* (1980); Bunn (1983); Abbott (1984); Abbott *et al.* (1984); Majer (1984, 1985); Postle *et al.* (1986, 1991); Abensperg-Traun & De Boer (1990); Abensperg-Traun (1992, 1993a); M Burns (1992; School of Environmental Biology, Curtin University, Perth, unpublished report); Little & Friend (1993); Abensperg-Traun & Milewski (1995); Abensperg-Traun & Perry (1995); Abensperg-Traun *et al.* (1993, 1996a,b,c,d).

Vegetation/disturbance	Sampling method						
	Soil trenching/ skimming	Soil cores	Litter cores	Litter quadrats	Pitfall traps	General hand search *	Baiting
Vegetation type							
Eucalyptus forest	0	5	2	3	1	1	0
Eucalyptus woodland	4	1	0	1	1	4	1
Banksia woodland	1	0	0	0	0	1	0
Mulga woodland/shrubland **	1	0	0	0	0	1	0
Heath/shrubland	3	0	0	0	1	3	0
Hummock grassland	1	0	0	0	0	1	0
Disturbance type							
Fire**	2	3	2	2	5	2	0
Livestock-grazing**	2	0	0	0	0	3	0
Regenerated farmland	1	0	0	0	0	1	0
Rehabilitated minesites	0	0	0	0	0	1	0
Pine plantation	1	0	0	0	0	1	0
Dieback	0	1	0	1	0	0	0
Habitat fragmentation	1	0	0	0	0	1	0
Pasture	1	1	0	0	0	1	0

* indicates mounds, standing/lying dead wood, roots, leaf litter, etc; ** indicates inclusion of broad termite survey of Davies (1970) for grazed mulga woodland/shrubland and Perry (1972) for burnt hummock grassland.

Table 2

Numbers of studies on fire effects with regard to sampling methods and vegetation types.
See Table 1 for source of data.

Vegetation type	Sampling methods					
	Soil trenching/ skimming	Soil core	Litter core	Litter quadrat	Pitfall-trap	General hand search
Eucalyptus forest	0	3	2	1	2	0
Eucalyptus woodland	2	0	0	1	1	2
Mallee	1	0	0	0	0	1
Heath/shrubland	4	0	0	0	1	4

quadrats/traps. All studies that used soil-trenching/skimming and hand-sampling were termite-only investigations (Table 3). The exceptions were two studies on the effects of habitat fragmentation and recolonization of regenerated farmland where a broad range of soil/litter arthropods were investigated. All other generalized arthropod studies used various combinations of the other methods (cores/ quadrats/pitfall-traps).

Sampling effort/regime

When totalling numbers of study sites for vegetation types where termite abundance and/or species richness was measured, eucalypt woodlands and heath/shrublands were sampled most extensively (Table 4). The least work

was for termite communities in eucalypt forests, *Banksia* woodland, mulga woodland/shrubland, mallee and hummock grassland. Two broad surveys listed termite species for mulga woodland/shrubland (Davies 1970) and hummock grassland (Perry 1972). Perry *et al.* (1985) listed species for the extreme south-west of the State (coastal and near-coastal forest and woodland ecosystems). There have been no termite community studies for rainforest vegetation in Western Australia.

The greatest number of study sites on disturbance effects were for livestock-grazing, habitat fragmentation, regenerated farmland, rehabilitated bauxite mines and fire (Table 4). The lowest numbers of sites addressed the influence of cultivation and dieback, and the effects of replacing

Table 3

Numbers of studies that used different sampling methods by termite-only studies, and by studies where a broad range of soil and litter arthropods, in addition to termites, were investigated. See Table 1 for source of data.

Sampling method	Type of study	
	Termites only	Broad range of arthropod taxa
Soil trenching/skimming	6	2
General hand search *	7	2
Soil cores	0	6
Litter cores	0	2
Litter quadrats	0	4
Pitfall-traps	0	3
Baits	1	0

* indicates mounds, standing/lying dead wood, roots, leaf litter, etc.

native vegetation with exotic, commercial timber such as *Pinus* pine (Table 4). No studies were conducted on the effects of replacing native vegetation with eucalypt plantations.

There was considerable variation between individual studies in the number of study sites, the number of sampling units within sites, and their dimensions (Table 5). There was also wide variation in the number of months/ seasons sampled (not shown). However, individual investigators showed some consistency in the number and dimension of their sampling units across different studies (*e.g.* soil cores in studies by Abbott (1984) and Abbott *et al.* (1984); soil trenches in studies by Abensperg-Traun 1992; Abensperg-Traun & De Boer 1990; Abensperg-Traun & Milewski 1994; Abensperg-Traun *et al.* 1996a,b). Diameters of pitfall traps showed least consistency across the different studies. Of 11 discrete studies that used a combination of soil/litter cores, litter quadrats and pit-fall-traps, four studies sampled two study sites only. These studies lacked treatment replication because all but one of these investigations compared termite abundance in unburnt and burnt vegetation (eucalypt forest). An additional four studies sampled three sites each of which two studies were on the effects of fire (Table 1, 2 and 5). All studies on fire effects are therefore based on data collected from three or less study sites. A study by Abensperg-Traun (1993a) sampled one site only but used high within-site treatment replications as a test of the efficiency of sampling wood-eating termites with different types of woody baits (Table 5).

Table 4

Total numbers of study sites (across separate investigations) at which termite abundance and/or species richness was assessed for vegetation and disturbance types. Source of data: [a] Abbott (1984); [b] Abbott & Parker (1980); [c] Abbott *et al.* (1984); [d] Abensperg-Traun (1992); [e] Abensperg-Traun (1993a); [f] Abensperg-Traun & De Boer (1990); [g] Abensperg-Traun & Milewski (1995); [h] Abensperg-Traun & Perry (1995); [i] Abensperg-Traun *et al.* (1993); [j] Abensperg-Traun *et al.* (1996a); [k] Abensperg-Traun *et al.* (1996b); [l] Bunn (1983); [m] M Burns (1992; School of Environmental Biology, Curtin University of Technology, Perth, unpublished report); [n] Davies (1970); [o] Little & Friend (1993); [p] Majer (1984); [q] Majer (1985); [r] Nichols & Bunn (1980); [s] Perry (1972); [t] Postle *et al.* (1986); [u] Postle *et al.* (1991); [v] Whelan *et al.* (1980); [w] Nichols *et al.* (1989).

Vegetation/disturbance	Total number of study sites	
	Termite abundance	Termite species richness
Vegetation type		
Eucalyptus forest	20 [aclpqtuv]	12 [l]
Eucalyptus woodland	58 [bdefgk]	53 [defgk]
Banksia woodland	0	11 [hi]
Mallee (*Eucalyptus* spp)	9 [bfg]	8 [fg]
Mulga (*Acacia aneura*) woodland/shrubland [1]	0	[n]
Heath/shrubland [2]	48 [fgio]	45 [fgi]
Hummock grassland [3]	0	[s]
Disturbance type		
Fire [3]	20 [acgopqv]	10 [gs]
Livestock-grazing [1]	35 [dk]	36 [dkn]
Regenerated farmland	27 [j]	27 [j]
Rehabilitated minesites	27 [mr]	27 [mrw]
Pine plantation	0	1 [h]
Dieback	1 [t]	0
Habitat fragmentation	29 [k]	29 [k]
Pasture [4]	4 [b]	2

[1] one broad termite survey by Davies (1970); [2] inclusion of mallee-heath and banksia scrub (from Abensperg-Traun & Milewski 1995); [3] one broad termite survey by Perry (1972); [4] Abensperg-Traun, unpublished.

Table 5

Dimensions of sampling units, numbers of samples per site and numbers of study sites used by individual studies. L = length, W = width/diameter, D = depth. Source of data: [a] Abensperg-Traun (1992); [b] Abensperg-Traun & De Boer (1990); [c] Abensperg-Traun & Milewski (1995); [d] Abensperg-Traun et al. (1996b); [e] Abensperg-Traun et al. (1996a); [f] Abbott et al. (1979); [g] Abbott (1984); [h] Abbott et al. (1984); [i] Majer (1984); [j] Postle et al. (1986); [k] Postle et al. (1991); [l] Majer (1985); [m] Whelan et al. (1980); [n] Little & Friend (1993); [o] Abensperg-Traun (1993a). Summary excludes general hand collections from microhabitats (wood, mounds, litter, etc).

Sampling units	Dimensions of sampling units (mm)	Number of sampling units per study site	Number of study sites
Soil trenches	1000 (L) x 100 (W) x 100 (D)	20	10[a]
	1000 (L) x 100 (W) x 100 (D)	20	18[b]
	1000 (L) x 100 (W) x 100 (D)	20	18[c]
	1000 (L) x 100 (W) x 100 (D)	20	27[d]
	1000 (L) x 100 (W) x 100 (D)	20	29[e]
Soil/litter cores	107 (W) x 53 (D)	8	3[f]
	106 (W) x 55 (D)	50	2[g]
	106 (W) x 55 (D)	50	2[h]
	54 (W) x 97 (D)	10	2[i]
	54 (W) x 97 (D)	10	2[j]
	54 (W) x 97 (D)	20	3[k]
Litter quadrats	190 x 190	10	2[i]
	190 x 190	10	14[l]
	190 x 190	10	2[j]
	190 x 190	20	3[k]
Pitfall traps	18 (W)	16	3[m]
	65 (W)	50	2[g]
	65 (W)	50	2[h]
	42 (W)	20	14[l]
	90 (W)	32	3[n]
	42 (W)	16	27[d]
	42 (W)	16	29[l]
Wooden stakes	600 (L) x 50 (W) x 50 (W)	15 *	1[o]

* indicates 15 replicates each for five wood species.

Discussion

General

Termite research in Western Australia has been biased towards vegetation types in the mediterranean south-west (eucalypt forests and woodlands, heath/shrublands). This bias reflects logistic difficulties of working in remote regions where mulga woodlands/shrublands, mallee and hummock grasslands often predominate. Emphasis on south-west ecosystems, however, ignores the bulk of Western Australia where the functional role of termites (and ants), relative to other taxa, is almost certainly the most important (Matthews 1976; Stafford Smith & Morton 1990).

With the exception of Davies' (1970) broad termite survey on Mileura Station, no study has been conducted on termite communities in the vast pastoral region encompassing most of the arid and semi-arid zone although analogous studies from interstate may provide some insights into termites under pastoral forms of landuse (e.g. Watson et al. 1973, 1978).

Several investigators have drawn attention to likely sampling deficiencies due to the typically aggregated distribution of termites in soil samples, and their paucity in litter samples and pitfall traps. Examples include .... "no data for a large number of soil cores" (Abbott 1984; Abbott et al. 1984); "because of the low numbers and patchy distribution of large soil animals, especially termites, ..., it is unrealistic to examine the statistical significance of differences ..... between virgin and farmed soil" (Abbott & Parker 1980); "numbers of Isoptera (in pitfall traps) were borderline for statistical analysis (Little & Friend 1993); "termites were captured only once in the litter and only occasionally in the soil" (Postle et al. 1986). The patchy distribution of termites in cores and litter quadrats was also noted by Majer (1984), and this is widely regarded as one of the major impediments to the effective quantification of the relative abundance of subterranean termite populations (Lee & Wood 1971; Sands 1972; Nutting & Jones 1990; Eggleton & Bignell 1995). Time of year at which termites were sampled may also have influenced sampling deficiencies (see below).

With the possible exception of optimal termite habitat such as some tropical grasslands and savannas, soil cores are rarely effective in quantifying subterranean termite populations, and extracting cores of adequate size (width and depth) are impractical and time consuming (Sands 1972; Eggleton & Bignell 1995). Soil trenches sample a

higher soil volume and, although causing higher distur-
bance to the soil and its biota, they are more likely to
provide statistically acceptable data (Kemp 1955; Bigger
1966). For example, the total soil volume sampled by 20
trenches per site in studies by Abensperg-Traun (*e.g.*
1992) was four times greater than the 50 soil cores per
site collected by Abbott (1984) and Abbott *et al.* (1984).
Soil cores have been used as a primary sampling method
in Australian studies, but these were supplemented with
additional sampling techniques aimed specifically at ter-
mites (*e.g.* Holt *et al.* 1993, 1996). For native earthworms,
which also have an aggregated distribution pattern in
the soil of jarrah forest, Abbott (1985) found an almost
perfect correlation between percent frequency of occur-
rence and total earthworm density in soil cores ($r^2 = 0.94$).
Whether the relationship between abundance/density
and frequency of occurrence also holds for the termite
fauna remains to be seen. Nevertheless, considerable ana-
lytical difficulties (high mean:variance ratio) remain in
analyzing termite abundance, even with data from soil
trenches (*e.g.* Abensperg-Traun & De Boer 1990). Low
efficiency of litter cores/quadrats was shown by the
studies of Whelan *et al.* (1980) and Majer (1984, 1985).
Pitfall-traps (which can assess harvester termite popula-
tions only) may only be used effectively where such termite
populations are large, and if trapping coincides with
peak harvesting times of the year (James 1991). Harvester
termites are particularly prevalent in arid and seasonally
arid tropical and sub-tropical regions (*e.g.* Watson & Gay
1970). Frequency of occurrence of termites summed
across soil trenches and surface wood/mounds, may also
be an inefficient measure of their relative abundance (*e.g.*
Abensperg-Traun & Milewski 1995; Abensperg-Traun *et
al.* 1996a), unless treatment differences are very consider-
able (*e.g.* Abensperg-Traun *et al.* 1996b).

When to sample?

The efficiency of soil-based assessments depends not
only on the size and density of sample units (cores,
trenches) but also on when samples are taken. Termites
are highly susceptible to fluctuations in soil moisture and
temperature conditions. Studies by Williams (1934) and
Abensperg-Traun & De Boer (1990) suggest a minimum
soil moisture requirement of about 3.5% to maintain
some activity near the surface where most sampling
occurs. At higher soil moisture levels, however, soil
temperature becomes the determining factor influencing
activity (Ueckert *et al.* 1976; Abensperg-Traun & De Boer
1990). Termite biomass near the soil surface in the central
wheatbelt of Western Australia, a semi-arid environment
with a highly variable climate, declined seasonally (in
mid-summer; February) by as much as 95% of its annual
peak (in spring; September), largely as a result of heat
and drought (Abensperg-Traun & De Boer 1990). Termite
species richness in soil trenches was highest following
the first good rains in autumn (April) and a rise in soil
temperatures in spring; spring and autumn sampling
yielded similar species numbers (Abensperg-Traun 1991).
Sampling at suboptimal times of the year will exacerbate
the effects of termite aggregation in the soil matrix , with
a relatively high proportion of samples containing no
termites. Ueckert *et al.* (1976) showed that termites
migrated to below 124 cm in the soil to avoid soil surface
temperatures of less than 10 °C. There is no evidence that
different termite species are active at different times of

the year. Nevertheless, unless sampling occurs at peak
activity periods, surveys should be repeated at several
times of the year.

What to measure

Abundance or species richness? Current methods of as-
sessing the relative abundance of subterranean termites
are laborious and time-consuming in both the field and
laboratory, and are often problematic in terms of mean-
to-variance ratios. They are therefore potentially unreliable
for comparative purposes (*e.g.* termites in grazed/
ungrazed, or burnt/unburnt vegetation). Is there some
other (surrogate) measure of termite abundance?

Abensperg-Traun & De Boer (1990) quantified soil-
inhabiting termites in the central wheatbelt by extracting
all termites from sample trenches (each trench about
5 000 cm³ of soil) for estimates of biomass and species
richness, across 18 study sites and three vegetation types
(20 trenches per site, monthly for 11 months). Sites with
relatively high mean termite biomass per trench also
supported relatively high numbers of soil-inhabiting
termite species (Fig 1). Because of a high mean-to-
variance ratio, a correlation analysis was unsuccessful in
linking biomass with species richness. A positive
relationship between abundance and species richness in
south-west ecosystems is not peculiar to termites, as
might be expected, but applies also to many other
invertebrate taxa; earthworms in jarrah forest ($r^2 = 0.42$;
Abbott 1985); cockroaches ($r^2 = 0.39$), earwigs ($r^2 = 0.82$)
and beetles ($r^2 = 0.62$) in gimlet woodlands (Abensperg-
Traun *et al.* 1996b); and ants in rehabilitated minesites ($r^2
= 0.71$; calculated from data in Majer *et al.* 1984). Termite
species richness may be a valid surrogate for termite
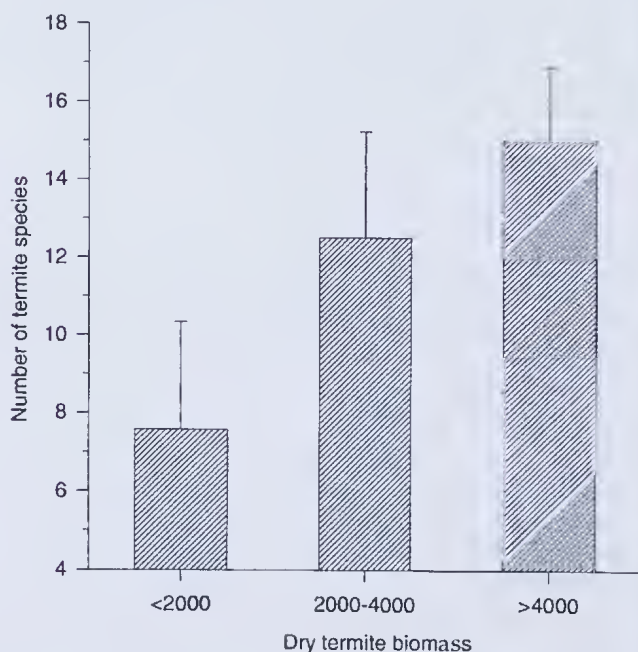abundance in these particular ecosystems.

Figure 1. Relationship between termite abundance (mean dry
biomass per sample trench per study site, ± sd) and termite
species richness in the soil (mean number of species per study
site, ± sd) across native habitats in the Western Australian
wheatbelt (six study sites each for wandoo *Eucalyptus capillosa*
woodland, mallee *Eucalyptus* spp and shrubland; data from
Abensperg-Traun & De Boer 1990).

For studies of disturbance effects, species richness may be a more appropriate variable than abundance to measure, because population decline may recover more readily than species loss, particularly in fragmented environments such as the wheatbelt (Abensperg-Traun *et al.* 1996b). Areas of disturbance (*e.g.* bauxite mines and clear-felled coups) nested within eucalypt forests of the south-west may not be constrained by fragmentation effects, however. This is because of adjacent native habitat for recolonization according to island biogeographic theory (MacArthur & Wilson 1967), and Majer *et al.*'s (1984) data on ants in rehabilitated bauxite minesites in south-west forest ecosystems.

Termite species richness is relatively easy to measure and species counts pose no analytical difficulties. However, a sampling regime focused on the soil alone (as in Abensperg-Traun & De Boer 1990) may not effectively sample the resident fauna in terms of species richness. For 27 shrubland sites in the central wheatbelt, for example, soil trenches failed to account for 18 termite species (out of a total of 51 spp; Abensperg-Traun *et al.* 1996a, Table 6), most of which were restricted to dead and decaying wood. Conversely, restricting sampling to wood will not effectively sample the harvester termite component in arid and semi-arid regions in particular, but may provide adequate measures of site richness in south-west forests where harvester termites are scarce (Perry *et al.* 1985). Pitfall traps showed very low efficiency at capturing site richness in wheatbelt habitats (Table 6). This may also apply to more arid and seasonally arid regions where wood-eaters are an important component of the fauna (Saunders 1969; Barrett *et al.* 1973; Watson *et al.* 1978; Braithwaite *et al.* 1988).

Table 6

Sampling effectiveness for assessing termite species richness using three different methods. Data are from 27 shrubland sites in Western Australia's central wheatbelt (Abensperg-Traun *et al.* 1996a,c).

	Pitfall traps	Soil trenches	General hand search *
Species recorded by method	4	28	31
Species not recorded by any other method	0	18	13

* indicates mounds, surface wood, roots, stumps, litter.

Soldier termites are necessary for species identification, so every effort must be made to collect them from each sample. Otherwise, species richness may be significantly underestimated. Some species have very low soldier:worker ratios (Haverty 1977; Abensperg-Traun 1993b). This applies particularly to the predominantly wood-eating *Amitermes* complex which is especially rich in species in shrubland ecosystems of the south-west (Abensperg-Traun & Steven 1997). Perseverence is therefore often required to locate such rare soldiers.

Generic richness? Identifying termites to genus is considerably easier than to species level, and this raises the question whether numbers of termite genera at any one study site effectively describe species numbers also. I examined this relationship for five ecosystem types from the south-west of Western Australia for which the data are adequate. These ecosystems varied in structural and floristic complexity, numbers of study sites, disturbance histories and species and generic richness (Table 7). After log transformation of species and genus numbers, generic richness was significantly correlated with species richness for each of the five ecosystem types (Table 7). Percent variations in species richness explained by genus richness were; wandoo woodland 39 %, shrubland 50 %, gimlet woodland 65 %, jarrah forest 90 % and rehabilitated bauxite minesites 95 %. Not surprisingly, highest percentage variations explained were for ecosystem types with the lowest richness of species and genera (Table 7) because the species-to-genus ratio approached 1. This applied to jarrah forests (mean species-to-genus ratio 1.08) and rehabilitated minesites (mean ratio 1.08). Species-to-genus ratios for other ecosystem types were 1.49 (gimlet

Table 7

Relationships between (log transformed) numbers of termite species and numbers of termite genera for a varying number of study sites across five different ecosystem types in the south-west of Western Australia; r is the correlation coefficient. Source of data: [1] Abensperg-Traun (1992, 1993a); [2] Abensperg-Traun *et al.* (1996b); [3] Abensperg-Traun *et al.* (1996a); [4] Bunn (1983); [5] Nichols & Bunn (1980).

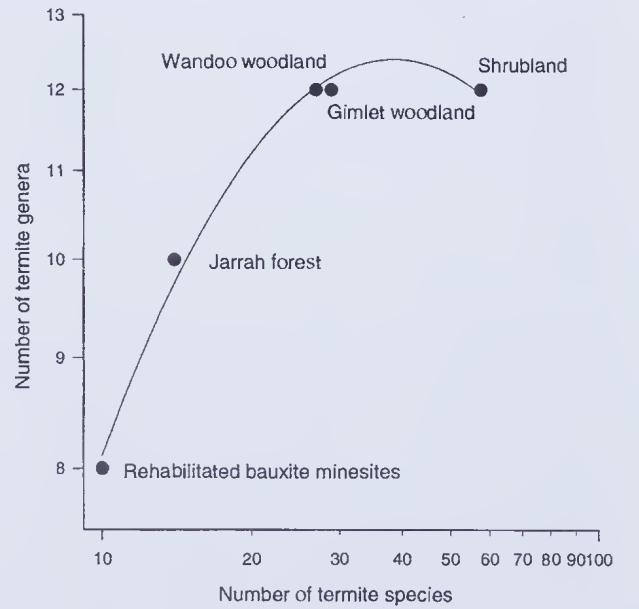| Ecosystem type	Termites Species	Genera	r	Number of study sites
Wandoo (*E. capillosa*) woodland [1]	27	12	0.622*	11
Gimlet (*E. salubris*) woodland [2]	29	12	0.806**	29
Shrubland [3]	58	12	0.706**	27
Jarrah (*E. marginata*) forest [4]	14	10	0.949**	10
Rehabilitated bauxite minesites [5]	10	8	0.974**	20

* $P < 0.05$, ** $P < 0.001$.

Figure 2. Logistic regression between termite species and genus numbers for five ecosystems types in the south-west of Western Australia (note log-log scale; data from Table 7).

woodland), 1.52 (wandoo woodland) and 1.66 (shrubland). The implication of these ratios is that the use of generic richness as a surrogate for species richness will be unreliable where few genera contribute the majority of species (typically *Amitermes* spp and *Tumulitermes* spp in arid and semi-arid regions). This relationship is consistent with the global pattern for the termites (Eggleton *et al.* 1994), and Australian ants (Andersen 1995). The relationship between total species and genus numbers across the different ecosystem types was highly significant, explaining 99 % of the variation in site richness (r = 0.996, n = 5, P < 0.001; Fig 2).

Future directions

The ecological framework for suggested future termite research in Western Australia emphasizes the broad topics of patterns and processes and focuses on what are considered to be the most important issues.

Patterns. While characteristics of soils (*e.g.* texture, structure) and vegetation (*e.g.* structure, floristic composition) are often cited as major factors influencing termite abundance and diversity (Lee & Wood 1971; Wood & Johnson 1986), most of these observations are unquantified. Given the complexity of many soils (e.g. patchiness of physical/chemical characteristics at all spatial scales) and plant communities (floristic heterogeneity), such as those in the southwest of Western Australia (Lamont *et al.* 1984; McArthur 1991), more detailed data are necessary for a better understanding of spatial patterns. Termite abundance or diversity has also been linked with soil nutrient levels (Ratcliffe *et al.* 1952; Goodland 1965; Ferrar 1982; Wood *et al.* 1982; Salick & Tho 1984; Braithwaite *et al.* 1988; Jones 1990) and microbial biomass of soils (Holt 1996) but causal relationships are acknowledged to remain poorly understood (Holt 1996). Our inadequate knowledge for purposes of ecosystem management extends to spatially extensive but poorly sampled vegetation types where research on the abundance and diversity of termites should be encouraged. They include hummock (spinifex) grassland, mulga woodland/shrubland, mallee and rainforest. Hummock grassland (*Triodia* spp and *Plectrachne* spp), for example, covers more than 50 % of mainland Western Australia (Beard 1969), and mulga (*Acacia aneura*) occupies much of the central third of the State, covering an estimated 700 000 km² (Morrisey 1984). Mallee vegetation (*Eucalyptus* spp) covers extensive areas in southern regions (Beard 1990), while rainforest is restricted to small and isolated remnants within a savanna matrix in the northern-most parts of Western Australia (McKenzie *et al.* 1991).

Poor understanding of the major driving forces determining spatial patterns of termite abundance and diversity is matched by our general lack of knowledge of the effects of fire. Given the important role of fire in ecosystem management in Western Australia, this represents one of the most serious short-comings of our current knowledge base. Whether natural or used as a management tool, fire is closely associated with two major Western Australian ecosystem types, eucalypt forests and hummock grasslands (Suijdendorp 1981; Friend 1995). Most eucalypt forests are burnt regularly for fuel reduction (Christensen & Abbott 1989), with rotations of 5 to 6 years for jarrah (*Eucalyptus marginata*), and 7 to 9 years for karri (*E. diversicolor*). For *Triodia pungens* in northern parts of Western Australia, a fire frequency of approximately once every five years has been noted and thousands of square kilometers are often burnt (Winkworth 1967; Suijdendorp 1981; Griffin 1992). Our understanding of fire effects on termite communities in hummock grasslands (for Australia as a whole) is limited to one anecdotal report of the local extinction of *Drepanotermes* harvesters in intensely burnt *Triodia angusta* on Barrow Island (Perry 1972; see also Abensperg-Traun *et al.* 1996c for a discussion of fire effects on the survival of colonies of the harvester termite *Drepanotermes tamminensis*). The only other Australian study on fire effects is an unpublished investigation by Hodda (1992) in tropical Australian savanna ecosystems which has no direct relevance to south-west forests or hummock grasslands in the arid zone.

Processes. The dynamic nature between termites and other elements of the ecosystem, emphasises two process-related issues; those related to habitat modification by termites, and those associated with the interaction between termites and other fauna. We understand reasonably well the extent to which termites modify soils which includes physical disturbance of soil profiles, changes in soil texture, the nature and distribution of organic matter and the distribution of plant nutrients (Holt *et al.* 1980; Park *et al.* 1994; Lobry de Bruyn & Conacher 1995). We also know that termite feeding activities affect plant growth and plant species composition via modification of soil properties (Spain & Okello-Oloya 1985; Spain & McIvor 1988; Andersen & Lonsdale 1990). Following a number of years of above average rainfall and a consequent increase in the availability of plant food, as well as populations of mound-building harvester termites, the combined effects of harvester termites *Drepanotermes perniger* and cattle during a subsequent drought has been linked with the degradation of a mulga (*Acacia aneura*) ecosystem. Increases in mound densities during good years led to almost contiguous areas where the hard pavement-like mound surfaces resisted erosion, plant growth and seedling establishment (Watson & Gay 1970; Watson *et al.* 1973). A subsequent study by Watson *et al.* (1978) suggests a longevity of up to 250 years for the mounds of *D. perniger*. The long-term effects of the combined activities of harvester termites and livestock on arid zone ecosystems are poorly understood yet are of considerable importance for production systems (pastoral industry) as well as ecosystem management for the benefit of native plants and animals.

Conversely, possible flow-on effects on nutrient-cycling and soil formation, for example, following a significant decline in termite abundance and diversity (*e.g.* see Abensperg-Traun *et al.* 1996b) remain unclear. There is a great paucity of empirical evidence linking declines in arthropod abundance and diversity in general, and that of termites in particular, with changes in rates of ecosystem function (Hobbs *et al.* 1995; Naeem *et al.* 1995). There may not be a rectilinear relationship between *e.g.* termite diversity and ecosystem function (*e.g.* rates of nutrient-cycling). The data of Springett (1976), for example, showed an asymptotic (logistic) relationship between the diversity of soil microarthropods and litter decomposition in pine plantations of the south-west of Western Australia. In other words, a minimum number of species may be required for full ecosystem function, while at some threshold additional species add little further function, other than as

an insurance policy in times of disturbance and change when a full compliment of species (and their functional characteristics) enhance ecosystem stability (Main 1981). The magnitude of flow-on effects following a loss of termite species and numbers would clearly depend on the severity of the decline, on density compensation by other termite species with comparable functional roles, and on the importance of termites relative to other soil and litter invertebrates. Where termites are high in numbers and species, particularly in arid and semi-arid regions, other macroinvertebrates (except ants) are less well adapted to the prevailing environmental conditions and are therefore comparatively minor components of the fauna in terms of numbers and biomass (Matthews 1976; Stafford Smith & Morton 1990). Here, detrimental flow-on effects on other components of the ecosystem are likely to be of much greater significance than in areas where termites are a minor component (Cushman 1995). However, a significant decline in termite abundance and diversity as a result of disturbance is likely to see a decline in some other groups also (Abensperg-Traun et al. 1996b).

Compared to ants which interact intensively with a wide range of other fauna, particularly as predators and competitors (Holldobler & Wilson 1990), termites are timid, cryptic and specialized foragers of plant matter, with comparatively few interactions with other invertebrates. The most apparent interactions involve their role as food for predators and as hosts for other fauna within their nest structures. Here also we have varying levels of ecological insights of the range, nature and intensity of interactions. Predation may occur at varying levels, namely on the nest, on individual foragers or on winged reproductives (alates) during their nuptial flight, involving vertebrates and invertebrates. The availability of termite alates in spring represents a major source of food for insectivores, ensuring the availability of large amounts of fat-laden food items at a time when most insectivores (birds, some mammals, reptiles and frogs) have initiated breeding activity and hence have elevated energy requirements (see also Discussion in Abensperg-Traun 1994). Predation may also occur from within the nest by termitophilous invertebrates (Watson & Gay 1991). Predation on termites by mammals and lizards is much better known than that of the invertebrates, particularly the ants with whom termites are known to have coevolved in an intense predator-prey relationship (see Holldobler & Wilson 1990 on the 'arms race' between termites and ants). In Africa, whose termite fauna resembles the Australian fauna in abundance and diversity, several ant species are termite-specialized (Longhurst et al. 1978, 1979), as are other invertebrates such as some spiders (Dippenaar-Schoeman & Meyer 1980; Eberhardt 1991; Jocque & Dippenaar-Schoeman 1992) and possibly several species of land planarians (Jones et al. 1990). Some aspects of the interactions between termites and ants in Australia are given by Greenslade (1970), Holt & Greenslade (1979), Higashi & Ito (1989) and Holt (1990), but our understanding of the extent and effects of ant (and other invertebrate) predation on termites deserves more intensive research.

Termite mounds are host to many small mammals, birds, reptiles, frogs and other invertebrates, including termites, using the mounds as shelter, breeding and feeding sites (Mitchell 1965; King & Green 1979; Spain &

Brown 1979; Braithwaite 1990). Some mound co-inhabitants (other termites, e.g. Ahamitermes spp, termitophilous beetles Drepanoxenus spp) have been recorded only from the mounds of particular termite species, suggesting host specificity (Gay 1955; Watson & Kistner 1985; Watson & Gay 1991). Some of these interactions may be more in need of research than others, but all deserve preservation as part of thoughtful and effective ecosystem management.

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